PREDATION BY ARGYRODES (THERIDIIDAE) ON SOLITARY AND COMMUNAL SPIDERS*

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Introduction

Species of Argyrodes Simon (Theridiidae) are best known as kleptoparasites in the webs of other spiders, particularly in the tropics (Exline 1945; Exline and Levi 1962; Kaston 1965; Vollrath 1976, 1978, 1979). They live in or near the webs of their hosts and take prey from the host's web. The methods used to take prey from the host vary for different species of Argyrodes and different host species. In some cases the Argyrodes take food which the host has left at the capture site or in the hub of the web. They may also take small trapped insects which are not normally used by the host (Robinson and Olazarri 1971). In other cases the kleptoparasites feed from prey while it is still in the jaws of the host spider (Robinson and Robinson 1973).

Temperate zone Argyrodes are also found in the webs of other spiders, where they are generally considered to be commensal or kleptoparasitic. However, some temperate zone species of Argyrodes have been observed preying on their hosts. Argyrodes fictilium (Hentz) was observed feeding on an Araneus sp. host (Exline and Levi 1962) and on Frontinella communis (Hentz) (Archer 1946). Lamore (1958) reported A. trigonum (Hentz) feeding on Mecynogea lemniscata (Walckenaer) and Wise (in press) reports the results of an experimental study of the impact of A. trigonum on a population of Metepeira labyrinthea (Hentz.) It may be that predation on other spiders is more important than kleptoparasitism for some temperate Argyrodes. This note supports that view by presenting observations of spider predation by two species of Argyrodes, A. fictilium and A. baboquivari Exline and Levi. In addition it compares the occurrence and predatory activities of A.

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fictilium, A. baboquivari and A. subdolus O. P.-Cambridge in the webs of solitary and communal spiders.

METHODS

These data were collected during a field study of social behavior of *Philoponella oweni* (Chamberlin) (Uloboridae) in South Fork Canyon (1979 and 1980) and Herb Martyr Recreation Area (1980) in the Coronado National Forest in the Chiricahua Mountains, Cochise Co., Arizona, from June through September 1979 and July 1980.

In 1979, approximately 100 *P. oweni* web sites, occupied by solitary females or by communal groups of females with interconnected webbing, were examined 2–5 times per week. *Philoponella oweni* is facultatively communal. That is, in one habitat both solitary individuals and communal groups can be found. During each census I recorded the number of *Philoponella* present at the web site as well as presence and activities of *Argyrodes*. In most cases the *Argyrodes* were collected as soon as they were found. When *Argyrodes* were observed in the webs of non-uloborid spiders, this too was noted.

RESULTS

Argyrodes were observed in the webs of other spiders on 14 of the census days, covering a period from June 20 to September 18. Argyrodes fictilium were observed in the webs of other spiders on 3 occasions, each involving predation on the host species: hatchlings of P. oweni, a large Frontinella species, and a second, unidentified linyphiid. Predation by A. baboquivari was observed in seven of 19 sightings in webs of P. oweni. Both adult male and female A. baboquivari were seen preying on adults, immatures and eggs of P. oweni.

In July 1980 three specimens of A. subdolus were collected: one from the web of a solitary P. oweni and one from the webbing of each of two communal groups of P. oweni. Since A. subdolus was rarely seen, and since no feeding behavior of any sort was observed, these three observations were not included in later calculations.

The occurrence of *Argyrodes* in the webs of *P. oweni* and predation rates on the host were calculated for solitary and communal *P. oweni*. Even though only 28% of the web sites, on average,

were occupied by communal *P. oweni*, 50% (10 of 20) of the *Argyrodes* observed were found in communal groups. The difference between the distribution of *Argyrodes* expected, given the proportion of solitary and communal web sites, and that actually observed is significant at p < 0.05. (Expected number of *Argyrodes* in communal groups is $0.28 \times 20 = 5.6$; expected number in solitary webs is 14.4; observed values are 10 and 10; chi-square = 4.80, 1 d.f.)

Although I observed too few cases of actual predation to perform statistical analysis, the same trend is seen. A disproportionate number (4 out of 8 or 50%) of the observed predatory events occurred in communal groups.

DISCUSSION

Spider Predation By Argyrodes

Other spiders are a significant element in the diets of Argyrodes fictilium and A. baboquivari. In particular, A. baboquivari is one of the most conspicuous predators on P. oweni in the Chiricahuas.

The methods used by the more strictly kelptoparasitic Argyrodes may preadapt them for predation on the host itself. Legendre (1960) believed that Argyrodes kleptoparasites avoid attack from their hosts by recognizing their approach and quickly moving away. Vollrath (1976, 1978, 1979) showed that the host's prey wrapping motions produce distinctive vibrations in the web, which Argyrodes elevatus Taczanowski uses to locate the captured prey items. The use of these host-generated signals both to determine the location of the host in the web and to avoid attack could preadapt the Argyrodes for safely stalking and capturing the host herself.

Large body size, relative to that of the hosts, could also act to make predation on hosts more feasible. Kleptoparasitic Argyrodes tend to be smaller than their hosts. For example, females of A. elevatus and A. caudatus (Taczanowski) are about 3.4 mm and 3.5 mm long, respectively (Exline and Levi 1962) while their araneid hosts, Nephila clavipes (Linnaeus) and Argiope argentata (Forskal), are 12–16 mm and 22 mm long (Kaston 1978). On the other hand, those Argyrodes that are known to prey on other spiders are the same size or larger than their hosts. For example, females of A. baboquivari are about 3.7 mm long and females of A. fictilium are 5.5–12.00 mm long. Prey species such as Philoponella oweni are 4.7–7.1 mm long (Opell 1979) and females of Frontinella communis

are 3.0-4.0 mm (Kaston 1978). Since A. subdolus females are 2.2-2.6 mm in length, I predict that they are commensal or kleptoparasitic in the webs of P. oweni, not predatory on the adult females.

Most of the observations of tropical kleptoparasitic Argyrodes, such as A. elevatus, have focused on their relations with large orbweaver hosts. It is possible that even these "classically" kleptoparasitic species behave as predators when they encounter smaller species of spiders and the spiderlings of large species. Two tropical Argyrodes, A. attenuatus (O. P.-Cambridge) and A. colubrinus (Keyserling) are known to spin a few dry, non-sticky threads which are used as resting places by ballooning spiderlings and male spiders, as well as by minute flies. These prey are not ensnared in the web; instead the Argyrodes uses its web as a platform on which to stalk these tiny prey (Eberhard 1979). In addition, Stowe and Vollrath report that Argyrodes will attack molting spiders of any size (Stowe, pers. comm.)

Predator-Prey Interactions Between Argyrodes and Philoponella. The distribution of Argyrodes in solitary and communal webs of P. oweni raises some interesting questions about the searching behavior of Argyrodes and the value of P. oweni communal groups in defense against predators.

1. Search behavior of Argyrodes. Argyrodes occur more frequently in communal webs of *P. oweni*. This may be because the Argyrodes encounter communal webs more frequently, or because they remain longer in communal webs once they find them. My sampling scheme did not distinguish between these two phenomena, but there is circumstantial evidence that both occur.

Three Argyrodes females were collected from communal group #24 (one each on July 5, July 9 and July 14) and two from communal group #7 (one each on July 11 and 15). Since the Argyrodes were collected as soon as they were found, these are separate encounters. On the other hand, over the 1979 field season no more than one Argyrodes was ever found in any solitary web. This indicates that Argyrodes are encountering communal webs more frequently than solitary webs. This may be because communal webs are larger, because they offer more effective cues to searching predators, or because both Argyrodes and communal Philoponella are selecting similar environmental features.

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In two cases there was evidence that an Argyrodes had killed more than one individual in a communal group. On July 6 a female Argyrodes baboquivari was found in a communal group feeding on a P. oweni female; a second P. oweni female, sucked dry, was present in the webbing nearby. On July 14, a female A. baboquivari was found feeding on a P. oweni egg case, with the mother of the egg case dead and partially consumed nearby. This implies that Argyrodes may remain longer in communal groups, perhaps because they represent a large source of potential prey.

2. Communal behavior and defense against predation. Groupliving is often interpreted as a means of defense against predators. (See Brown 1975 and Wilson 1975 for summaries of this literature.) Of the many anti-predator strategies made possible by group-living, three could conceivably operate in communal spider groups such as those of *P. oweni*. These are enhanced detection of predators by groups of individuals; cooperative defense against predators; and the "selfish herd" effect.

The first two of these anti-predator strategies have not been observed in *P. oweni. Philoponella* do not appear to detect *Argy-rodes* in their webs. *Argyrodes* are frequently seen resting unmolested in both solitary and communal webs of *P. oweni.* No active defense behavior has been observed in the solitary or communal webs. *Argyrodes* feeding on one colony member were never approached by other colony members, and female *Philoponella* did not attack *Argyrodes* that were preying on their hatchlings.

The third anti-predator function of groups is the selfish herd effect (Hamilton 1971). If a searching predator encounters a solitary prey individual, that individual is likely to be attacked. When confronting a group, a predator may attack one individual, but the others are at least temporarily safe. The larger and denser the group, the smaller the probability that one particular individual will be taken by a predator.

My data are insufficient to determine if this is an important factor in *Philoponella* colonies. If an *Argyrodes* in a communal group takes only one or a few prey, then large communal groups may confer a certain amount of safety on their members through the selfish herd effect. But if the *Argyrodes* take many prey relative to colony size then the selfish herd is more like a collection of sitting

ducks. Since in this study the Argyrodes were removed from *Philoponella* webs as soon as they were spotted, the number of prey normally taken is not known.

Although it is clear that Argyrodes occur more frequently in communal webs than in solitary webs, and that a disproportionate number of predation events occurs in communal groups, it is not possible to say whether an individual P. oweni is safer (on the average) in a solitary web or in a communal group. The more hosts per colony an Argyrodes takes, the safer solitary webs become for the average Philoponella.

The biology of Argyrodes in both temperate and tropical climates deserves more study. They are an excellent group in which to study the evolution and ecology of various prey-capture techniques. Along with communal and gregarious host species such as Philoponella, they may provide a model system for the study of resource utilization in patches of different sizes.

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